AN ANATOMICAL STUDY OF THE EAR OF THE LIZARD,
COLEONYX VARIEGATUS

by

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>4</td>
</tr>
<tr>
<td>OBSERVATIONS</td>
<td>5</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>10</td>
</tr>
<tr>
<td>Maintenance of the tension of the tympanum</td>
<td>10</td>
</tr>
<tr>
<td>Compensatory mechanisms of the tympanum, hyoid apparatus, and tongue</td>
<td>11</td>
</tr>
<tr>
<td>Similarities between the geckos and pygopods</td>
<td>12</td>
</tr>
<tr>
<td>Significance of the connection of the hyoid with extracolumella</td>
<td>14</td>
</tr>
<tr>
<td>The transmission of ground vibrations to the otic capsule</td>
<td>17</td>
</tr>
<tr>
<td>Morphological similarities of the middle ear of geckos and pygopods</td>
<td>19</td>
</tr>
<tr>
<td>The effect of environmental stress on the middle ear</td>
<td>22</td>
</tr>
<tr>
<td>The evolution of vocal communication</td>
<td>24</td>
</tr>
<tr>
<td>SUMMARY AND CONCLUSIONS</td>
<td>26</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>28</td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Ventral view of the pharyngeal cavity and upper palatal region with the floor of the pharynx and tongue removed.</td>
<td>31</td>
</tr>
<tr>
<td>2.</td>
<td>Enlarged view of the extracolumellar insertion plate and columella. The facial artery pierces the footplate of the columella.</td>
<td>32</td>
</tr>
<tr>
<td>3.</td>
<td>Lateral view of the pharyngeal wall and external ear.</td>
<td>33</td>
</tr>
<tr>
<td>4.</td>
<td>Diagram illustrating the tympanic compensation for tongue and hyoid movements.</td>
<td>34</td>
</tr>
</tbody>
</table>
INTRODUCTION

The ground gecko, *Coleonyx variegatus*, is one of the few lizards which are known to make vocal sounds. Underwood ('54), in his comprehensive study of the superfamily Gekkonoidea, mentions that one of the diagnostic characteristics of this group is the possession of a voice. He further states that *Coleonyx variegatus* and *Eublepharis hardwickii* (family Eublepharidae) "...both have a loud voice. They do not utter single croaks but a long drawn out rattle...", which Underwood had not heard in any other gecko families.

When it was established that one of the individuals used in this study produced sound, it was postulated that voice communication might occur. If so, some type of phonoceptor should be evident in these lizards.

A review of the literature of the reptilian ear indicates considerable work has been done recently on the morphology of the inner ear (Shute and Bellairs, '53; Hamilton, '60).

The morphological foundations of the middle ear were laid down by Versluys ('98). His massive work included the descriptions of the middle ears of thirty-two species of lizards. However, after Versluys, little was added to the literature of the anatomy of this region until the
work of Smith ('38). More recently, works by Norris and Lowe ('51), Oelrich ('56), and Earle ('61) have described the middle ear of lizards in certain agamid and iguanid lizards.

Initial dissections of the middle ear of *Coleonyx variegatus* show that the posterior edge of the tympanum is not supported by the depressor mandibulae muscle. Instead, it is attached to the terminal projection of the hyoid arch, the epihyal. Romer ('56) in illustrating the hyoid apparatus of a gecko shows the tympanum in this position, but mentions nothing about the significance of this attachment. Since the epihyal is in direct contact with the rest of the hyoid apparatus in *Coleonyx variegatus*, movement of the apparatus could change the tension on the tympanum.

The present investigation considers the effect of movement of the hyoid apparatus on the tympanum. A discussion of the compensatory movements which hold the tympanic membrane taut during tongue and hyoid movement is included. In addition, morphological findings which may be of taxonomic value have been evaluated. They are related to a discussion of how the environmental stresses on these parts may explain their evolution. Finally, the part that the middle ear might play in communication between geckos is briefly discussed.

I wish to express my sincere appreciation to Dr. Robert B. Chiasson for his guidance and encouragement throughout this
investigation. I also want to thank the faculty members and graduate students of the departments of Zoology, Speech, and Psychology for their kind assistance.

A special note of thanks is extended to Dr. Mary T. Caldwell, Professor of Pharmacology, whose friendship and general counselling has been invaluable to me, and to Dr. Charles H. Lowe, Jr. and Dr. Peter E. Pickens, Department of Zoology, for their constructive criticism of the manuscript.
MATERIALS AND METHODS

Several preserved specimens of *Coleonyx variegatus bogerti* from the vicinity of Tucson, in southern Arizona, were obtained from Dr. Charles H. Lowe, Jr. These were examined with the aid of a binocular dissecting microscope. Heads of other preserved specimens were decalcified, using a solution of 10 ml. of concentrated nitric acid in 90 ml. of 70% alcohol, to which one gram of phloroglucin was added. Dioxan was used to dehydrate the tissues and the heads were embedded in paraffin. All the preceding steps were carried out under vacuum. Sagittal and transverse sections were prepared using Mallory's Triple connective tissue stain (Guyer, '53).

Demonstration of the cervical arteries was accomplished by ventricular injection with vinyl latex.

The terminology used in describing the musculature is that of Edgeworth ('35), while the terminology for the skull and hyoid apparatus follows Kluge ('62).

Several living animals were observed in a terrarium and with a dissecting microscope.
OBSERVATIONS

The middle ear is easily exposed by reflection of the ventral hyoid and throat musculature. The middle ear cavity is in direct, open communication with the relatively large pharynx (Figure 1).

The columella and extracolumella may be observed in situ (Figure 2). The footplate of the former inserts into the membrane covering the fenestra ovalis, extending laterally to its junction with the extracolumella (Figure 2). It is supported by a reflection of the tympanic epithelium, similar to the columellar fold described by Oelrich ('56). This fold is attached to the dorsal wall of the middle ear cavity.

No processus internus or processus dorsalis occurs at the junction of the bony columella and the cartilaginous extracolumella. The most distal end of the extracolumella expands into the familiar cross or X-shaped pattern described by DeBeer ('37). The pars inferior is the longest of the four processes, and the pars accessorius anterior is divided distally into two prongs (Figure 2). The posteriorly and dorsally directed pars superioris is attached by a ligament to the paroccipital process (Kluge, '62), with a few strands of this ligament inserting into the dorsal exterior surface of the quadrate. The pars
accessorius posterior is the shortest of the four processes and is directed posteriorly and ventrally.

The internal carotid artery passes ventral to the footplate of the columella. It gives off a rather large branch, the facial artery, which passes dorsally, penetrating the two-pronged attachment of the columella to the footplate (Figure 2).

The larynx is similar to the description by Kluge ('62) and Chiasson (personal communication). Chiasson describes vocal cords extending posteriorly from the arytenoid to the dorsal inner surface of the cricoid cartilage. There is no epiglottis and the cartilage rings of the trachea are complete.

The hyoid apparatus was generally found to be as described by Kluge ('62). The connection between the second epibranchial and the paroccipital process of the opisthotic was not found, however. In some specimens, a short cartilaginous connection was observed between epibranchial one and epibranchial two, passing posteroventrally from the former at a forty-five degree angle. The semi-lunar shaped epihyal is attached dorsally to the paroccipital process, and ventrally to the retroarticular process of the articular, both attachments being ligamentous (Figure 4). A triangular pharyngeal wall, supported beneath by the epihyal and epibranchials one and two, attaches by fascia to the adjacent muscular and skeletal elements (Figures 3 and 4).
The horizontal side of the pharyngeal wall is bounded by the ventral hyoid and throat musculature, including the episternohyoideus and the geniohyoideus. The apex of the triangular wall is formed by the junction of the horizontal episternohyoideus with the capiti-cleidoepisternalis. The vertical base of the triangular wall is formed by the retroarticular process of the lower jaw, a ventral portion of the quadrate bone, and dorsally by the adductor mandibulae muscle (Figure 4). The external opening of the ear occurs as a small oval opening in the pharyngeal wall just posterior to the otic notch of the quadrate.

A strip of constrictor colli which supports the pharyngeal wall passes anteroventrally from the dorsal fascia of the neck and inserts into the main portion of the posterior mylohyoideus. The fibers of this muscle are parallel to those of the depressor mandibulae. Beneath this muscle the stylohyoideus is seen to insert into the dorsal tip of the epihyal, as described by Camp ('23). Its fibers originate from the posterior mylohyoideus and pass dorsoanteriorly and externally around the wall and back to their origin. Another strip of the constrictor colli passes deep to the stylohyoideus, originating from the dorsal tip of epibranchial one and the body of ceratobranchial one. The fibers pass anteroventrally and join the main portion of the posterior mylohyoideus (Figure 4). The anterior mylohyoideus is as described by Camp ('23) with intermittent bundles of the geniohyoideus piercing it.
Before the constrictor colli and depressor mandibulae muscles were removed, a smaller triangle was observed bounded posteriorly by the anterior margin of the depressor mandibulae, anteroventrally by the posterior margin of the adductor mandibulae, and ventrally by the pterygoideus muscle. This triangle encloses the part of the pharyngeal wall which contains the external opening of the ear.

The external surface of the tympanum attaches posteriorly to the semi-lunar shaped epihyal, apparently splitting off from part of the exterior pharyngeal wall in this region. Thus, from the epihyal forward the pharyngeal wall splits, the outer part attaching to the previously described structures forming the vertical base of the triangle. The tympanum attaches to the inner surface of the epihyal, thus forming the second wall of a blind pouch. The tympanum also extends forward to its insertion on the mid-posterior surface of the quadrate.

In some specimens a small tympanic ligament occurs; it is similar to the one described by Willard ('15) for Anolis carolinensis. This ligament passes horizontally from its origin on the dorsal tympanic cavity wall to its insertion into the processus accessorius posterior to the extracolumella.

No laxator tympani muscle was observed. Versluys ('98) named this muscle according to its function. It is said to extend caudad, originating from the insertion of the tympanic ligament on to the extra-
columella and inserting into the connective tissue covering the paroccipital process.

Endolymphatic sacs, similar to the calcium glands described by Ruth ('18), were observed in one gravid female. These structures, according to Ruth (p. 314-15), are "...undoubtedly an auxiliary to the auditory organ, inasmuch as it supplies a calcium salt for the formation of the otoliths of the ear....it may be possible that this gland, during pregnancy, becomes more active, thus increasing the keenness of the auditory sense rendered necessary at that time for the protection of the parent and her progeny. On the other hand, there is evidence to show that the calcium gland prepares the calcium salt that is carried by the blood stream to the oviduct, where it is deposited as the shell surrounding the egg substance."
DISCUSSION

Maintenance of the tension of the tympanum:

A pumping motion in the ventral hyoid region of living specimens was observed. The rate of this pumping varied, becoming quite rapid if the animal was startled. The pharyngeal walls previously described, seem to function in a manner similar to that of a bellows system. Von Geldern ('19) wrote on the possible mechanism of the production of the throat-fan in Anolis carolinensis. He mentions a report which states that preceding the distension of the fan in Colotes versicolor, the animal swallows air and distends its dilatable pharynx. This seems to be similar to the process going on in Coleonyx variegatus. This distension of the pharyngeal wall may also cause an increase in the tension on the tympanum, causing it to bulge out. Camp ('23) noted that Coleonyx is the only genus so far known in which the three complete branchial arches remain. The arches in these animals provide a flexible and supportive skeleton for the distensible pharyngeal wall.

Another possible mechanism by which the tension of the ear drum may be maintained is by the straightening and/or enlarging of the artery piercing the columella. Increased heart rate during times of
excitement could result in temporary pressure changes in the artery. The arterial change would probably cause an increase in the tension of the tympanum and an increase in the rigidness of the columella, by forces exerted on the footplate and the forked insertion of the columella (Figure 2).

Compensatory mechanisms of the tympanum, hyoid apparatus, and tongue:

The pumping motion in the ventral hyoid region did not move the tympanum in either an anterior or posterior direction. However, extension of the tongue caused the tympanum to relax so that a slight folding of its surface was observed.

Three possible methods for combating the forward movement of the hyoid apparatus caused by extension of the tongue may be considered.

First, the epihyal which supports the posterior margin of the tympanum is attached by small ligaments both dorsally and ventrally. These attachments would tend to minimize the motion of the epihyal, although they by no means are strong enough to prohibit all movement.

Secondly, a muscular cross-bar support is formed, between the lateral portions of the hyoid and first branchial arch, by the stylohyoideus and a layer of the constrictor colli deep to the stylohyoideus (Figure 4). The fibers of these muscles join with those of the posterior
mylohyoideus. The simultaneous contraction of these muscles would tend to pull the dorsal tip of the epihyal towards the epibranchial, which in turn is pulled towards the epihyal by the deepest layer of constrictor colli. This results in an over-all reduction of the forward pull exerted on the hyoid apparatus by the musculature extending the tongue.

A third method of reducing the forward pull on the hyoid apparatus would be the cartilaginous connection between the first and second epibranchials (Figure 4). This connection is strengthened by the action of the episternohyoideus muscles, which are antagonistic to the protruders of the tongue and the genioglossi and geniohyoid muscles, which pull the hyoid apparatus forward.

**Similarities between the geckos and pygopods:**

Underwood ('57) shows many similarities between the geckos and the pygopods, in his work on the lizards of the family Pygopodidae. His description of the hyobranchial skeleton of the pygopods *Pygopus lepidopodus* and *Lialis burtonis* show them to possess complete first and second cartilagenous arches and portions of the third arch. This disagrees with Camp ('23) who mentions that all traces of the third arch are lost in this family. In fact, the hyobranchial apparatus of *Delma fraseri* is the most complete of the pygopods studied, and is very similar to that of *Coleyx variegatus*. 
In *Coleonyx*, the mylohyoideus anterior has the same inter-digitations with the geniohyoideus muscle as in most of the pygopod species which have been studied. Moreover, Shute and Bellairs ('53) show the similarity of the cochlear apparatus in geckos and pygopods. Of all of the lizards they examined, only the cochlear apparatus of the Teiid (*Tupinambis*) partially resembled that of the geckos and pygopods.

When thinking in terms of the general morphological appearance of the pygopods and the geckos, it would be very hard to conclude that the groups are related to each other. The former is composed of highly modified snake-like lizards restricted to Australia, possessing a greatly elongated body and limbs which are absent or strongly reduced. On the other hand, the geckos possess a chunky body with four limbs always present; they are climbers living in trees, or among rocks, and are widely distributed throughout the tropics and subtropics.

Recent work, however, shows a number of similar characteristics possessed by members of both groups. Absence of osteoderms, reduction of temporal arcades, and possession of a vertical pupil are three of these morphological characters. Shute and Bellaire ('53) state that it is possible that "...the geckos and pygopodids have both been derived from a group of common ancestors which had itself become distinct from the other lizards."
Significance of the connection of the hyoid with extracolumella:

Camp ('23) mentions that in many geckos, the primary connection of the hyoid with the extracolumella has been lost. This break leads to the dorsalwards migration of the epihyal to reach its new point of attachment, the paroccipital process. This migration carries the stylohyoideus muscle with it, where it is now found attached to the dorsal tip of the epihyal.

It could be postulated, that this freeing of the extracolumella from the rest of the hyoid resulted in the separation of the pharyngeal wall in this region into two layers. The inner of these two layers formed the outer wall of the tympanum, but it is never completely separated from its original attachment to the pharyngeal wall. The two layers of the wall attach to the epihyal. The freeing of the extracolumella from the rest of the hyoid apparatus allows the former to vibrate more freely. This explanation may reveal the manner in which the development of the tympanum took place in geckos.

A similar type of development may have taken place in the pygopods, which possess an external and middle ear. *Pygopus lepidopus*, according to Camp ('23), is the only limbless lizard which is a climber. Thus, possession of a tympanum to receive air-vibrations would be of obvious selective value.

If the middle ear of *Coleonyx variegatus* is assumed to be similar to that of the common ancestor of the geckos and pygopods, then an
explanation for the type of ear found in *Aprasia pulchella* is necessary. This pygopod has no tympanum, and the stapes is reduced to a tiny nodule of bone, presumably a vestige of the footplate of the stapes (Underwood, '57).

The breaking of the extracolumella from the rest of the hyoid apparatus, need not be interpreted as functioning for the reception of air-vibrations alone. Camp ('23) describes the unusual forward growth of the extracolumella into the spongy tissue of the upper and lower lips in the amphisbaenid lizards. The extracolumella has lost its connection with the rest of the hyoid apparatus (if it ever had one to begin with) and transmits vibrations from the side of the head and lower jaw directly to the mobile stapes. Camp ('23) says that this adaptation is of a highly specialized nature, and discards the once-held idea that the extracolumella was actually the epihyal and represented the most primitive connection of the entire hyoid arch known in adult reptiles.

The amphisbaenids are blind, fossorial lizards, showing great morphological variation. Yet, they possess vertebrae with subcentral arterial foramina similar to those of geckos and pygopods; they have no osteoderms, and a pierced columella is present here as in many geckos. They have many resemblances to the Teiidae; while these are for the most part secondary resemblances, they are, nevertheless, indicative of ancestral relationships. It will be remembered that one member of
the Teiidae (Tupinambis) had a cochlear apparatus similar to the geckos and pygopods. The Teiids also lack osteoderms. Thus, many characteristics used by Camp for his major divisions of lizards into Ascalabota and Autarchoglossa are observed to be shared by the above families. Superficial morphological appearances which make certain groups look diametrically opposed to one another may be misleading.

In discussing the evolution of the middle ear of Aprasia pulchella from a common ancestor, I shall consider the middle ear of the living Coleonyx variegatus as being similar to that of the common gecko-pygopod ancestor. This may be acceptable, for the members of the superfamily Gekkonoidea are sometimes considered to be the most primitive of all the living lizards. Camp ('23) indicates this by the use of his Paleotelic Weight to measure the relative primitiveness of the characters of the lizards.

The pars inferior of the extracolumella in the specimens of Coleonyx variegatus examined, was very long and slender. It almost touched the concave posterior surface of the quadrate, and it is not hard to imagine that this process once attached there, i.e., to the quadrate. In fact, it is possible that this process actually corresponds to the processus internus found in many other lizards. De Beer ('37) speaks of the presence of a processus internus in geckos, while Underwood ('57) states that none is present. Earle ('61) postulates that the expanded
knob of the extracolumella he observed in Holbrookia and Callisaurus represents the internal process in other lizards. Thus, a mechanism for the transmission of ground vibrations may be from the lower jaw, through the quadrate bone and then to the columella via the processus internus of the extracolumella. This could be the transmitting mechanism in some primitive pygopods whose tympanum is no longer functional.

The transmission of ground vibrations to the otic capsule:

If the columellar apparatus degenerates to the extent found in Aprasia pulchella, three possible mechanisms remain by which ground vibrations could reach at least the bones of the ear capsule.

The epihyal of the pygopods hyobranchial apparatus attaches to the paroccipital process as in geckos. In the specimens of Coleonyx variegatus examined, a broad lappet-like structure of the hypohyal comes in very close contact ventrally with the medial side of the lower jaw bone. Vibrations from the lower jaw, via the hyoid arch may reach the ear capsule.

Also of interest in the species of Coleonyx examined, is the attachment of the pars superior of the extracolumella insertion plate to the paroccipital process by a short ligament. This could represent a further adaptation of the above-mentioned mechanism, whereby ground vibrations could be brought not only to the opisthotic bone of
the ear capsule, but to the columella through the ligament of the pars superior. Of course, this would only function in pygopods which still have the insertion plate of the extracolumella present and would not be applicable to *Aprasia pulchella*. It is possible that this ligamentous connection of the pars superior process to the paroccipital process is the remains of the processus dorsalis described by De Beer ('37). It was observed that a few fibers of this ligament attaches to the dorsal exterior edge of the quadrate bone. These may represent what is left of the processus paroticus which De Beer ('37) describes as being derived from the processus dorsalis. The processus paroticus is a cartilaginous nodule between the articular head of the otic process and the wall of the auditory capsule.

A second mechanism by which ground vibrations may reach the ear capsule is represented by a chain of bones. Kluge ('62) describes the quadrate as serving as the basis for articulation between the cranium and the lower jaw. Thus, ground vibrations from the lower jaw and its surrounding tissues could pass through the quadrate to the ear capsule. Both the opisthotic and prootic bones articulate with the quadrate dorsally. Although the above description applies to observations on *Coleonyx variegatus*, a similar mechanism may function in other forms.

The position of the columella cranii (epipterygoid) in the geckos may serve as a means of transmitting ground vibrations from the lower
jaw to the prootic bone. However, this mechanism would probably not be of value to several of the pygopods, since this bone is usually reduced or even absent in burrowing lizards.

**Morphological similarities of the middle ear of geckos and pygopods:**

The fact that the columella is pierced for the passage of an artery, plus the similarity in connection of the ceratohyal to the otic capsule in both geckos and mammals, may be highly significant. Perhaps, the common ancestor of the mammal-like reptile and the primitive geckos had a middle ear apparatus similar to that observed in *Coleonyx variegatus*. Versluys ('98) hints at this possibility in the introduction of his work on the middle ear of Lacertilia and Rhynchocephalia (p. 164).

Der Stapes ist bei einigen Geckoniden zum Durchtritt einer ziemlich starken Arterie durchbohrt. Hierin sehe ich eine sehr alte Einrichtung, die den Vorfahren der Amnioten zukam, jetzt nur noch bei einzelnen Lacertiliern, bei sehr vielen Saugern und, vielleicht, bei vielen Vogeln erhalten ist.

Underwood ('57) proposes that even though many similar characteristics between the geckos and pygopods have been found, the pygopods were not derived from the gecko stock. They are definitely a stock of ancient origin and appear to have a common ancestry with geckos prior to any surviving gecko stock. The geckos are regarded as being very primitive.
At this point one may ask: What about parallel evolution as an explanation for the similarity of some morphological developments in the geckos and pygopods? Underwood ('57) warns that a simple list of characters of two seemingly related groups is not sufficient (p. 261).

I think that parallel evolution due to similar genetic changes on a similar genetic background is far too simple an idea to have more than a very limited application at the very lowest taxonomic levels.

In related stocks it may be reasonably assumed that the organization of development is similar. The course of development might be easily susceptible of modification along certain lines by small change in timing or intensity of a factor....Where such a change has no apparent direct adaptive significance its occurrence in two stocks may afford evidence of affinity.

He uses the passage of the facial artery anterior to the imperforate columella as an example of a change which has no apparent direct adaptive significance. This occurs in Sphenodon, snakes, pygopods and at least three stocks of geckos, while in most Autarchoglossa, and Agamidae, Chamoeleonidae, Iguanidae, and Xantusiidae, the artery passes posterior to the columella. Underwood ('57) further states (p. 262) that:

Parallel changes of adaptive significance are of uncertain value in discussions of affinity. We may expect such changes to occur in related stocks because similar evolutionary opportunities are open to organisms which are themselves similar by virtue of phyletic affinity.... Detailed study of such features may reveal beneath a superficial similarity, differences of organization which bear a roughly inverse relation to the closeness of affinity of the stocks.
The most valuable characters are special features which are confined to a few stocks. If they survive considerable adaptive modification of other parts of the organization then they are even more impressive.

An example of such a character would be the cochlear apparatus discussed by Shute and Bellairs ('53). These investigators also seem wary of using parallel evolution to explain their findings and feel that the striking and almost identical peculiarities affecting a relatively conservative organ such as the inner ear are unlikely to have been evolved independently in two distinct groups. They propose the explanation that the geckos and pygopods both have been derived from a group of common ancestors, which had itself become distinct from other lizards. Any major differences between the two groups are attributed to adaptations occurring after the separation of the two groups from their common ancestor stock. They further state that "...It is of course clear that the geckos, despite the fact that they have evolved certain specializations that are not seen in pygopodids, are on totality of characters more primitive than the latter and must show a closer approximation to the condition of the common ancestors of the two families."

The similar appearance of the facial artery in some geckos and pygopods, along with the similarity of the hyobranchial apparatus in these two groups, may be examples of changes which have no apparent direct adaptive significance. These may afford evidence of affinity between the families. However, the middle ear is highly adaptive. Any
similarities in this apparatus between the geckos and pygopods might easily be explained as having been acquired independently as a result of parallel evolution. Therefore, caution must be exercised in evaluating evolutionary affinities through morphological similarities of the middle ear. It seems logical that differences in the conservative inner ear would have more bearing in a consideration of the phylogenetic history and affinities of groups than the more highly adaptive middle ear.

The effect of environmental stress on the middle ear:

Methods of adaptation of the middle ear to certain environmental stressors have been proposed above, using Coleonyx variegatus as the representative of the common ancestor of geckos and pygopods. As Underwood ('57) maintains, what is important is that the adaptation shall function well in the life of the organism. This may or may not have been a part of Smith's ('38) point when he stated (p. 549) for certain lizards:

It seems reasonable to assume that, in having suffered loss of the tympanum and the structures that are attached to it, they cannot hear as well as before. There is nothing in their behavior, however, as far as can be seen, to indicate that they are handicapped by this. Whatever they have lost they seem able to get along very well without it.

Indeed, the animals may not have suffered at all, and if increasing the size of the depressor mandibulae muscle for more efficient burrowing
brings about a degeneration of the middle ear, then the former adapta-
tion has a greater selective value than the latter, with regard to the
survival of the organism as a whole. Also, the fact that the animals do
not seem to show any behavioral differences, seems to indicate that
some of the other sensory organs have compensated for the decrease
or complete loss of hearing.

Smith ('38) says that an orthogenetic view seems to explain the
degeneration of the ear in organisms that should benefit in having good
hearing power. However, the suggestion of Norris and Lowe ('51) that
"It seems possible that this degeneration has been the result of envir-
onmental stresses which, through selection, have brought about changes
in the musculature surrounding the tympanum,..." is a better explana-
tion of what is actually occurring. Smith ('38) may also want to con-
sider the degeneration of the ear in the pygopod _Aprasia pulchella_ as a
significant snake-like characteristic of the lizards, along with the
elongation of the body and degeneration of the limbs which has occurred
in the pygopods. He would probably explain this degeneration as a
result of orthogenesis. However, this view could not explain the reten-
tion of a well-formed tympanum in _Pygopus lepidopus_, the only known
limbless climber, or in _Lialis_ sp., the surface dweller which catches
and swallows other lizards (Camp, '23). It seems that the explanation
of Norris and Lowe ('51) of the importance of environmental stress on
the fate of the ear could also be used in these cases of the pygopods.

The evolution of vocal communication:

Bast and Anson ('49, p. 379) in their introduction to a historical survey of the internal ear say, "The perception of external stimuli is a problem which has always intrigued philosophers and scientists. This is especially true of the problem 'How do we hear?' Of all the organs for sense perception the ear is the best protected, the most delicate, structurally the most complicated, and functionally the least understood."

The well-developed ear and ability to produce sound in Coleonyx variegatus, as in any vertebrate, also leads one to the question of whether vocal communication is taking place between members of the species. If definite communication could be demonstrated, then the gecko might represent a primitive ancestral stage serving as an important link in the evolution of vocal communication between lower and higher vertebrates.

Evans ('36, p. 188) describes the vocal "chirping" of the breeding calls of two members of the family Gekkonidae, and from the observation of the courtship behavior, says that: "These details emphasize the fact that the gecko behavior is definitely correlated with vocal expression. This presupposes a receptor organ of extensive development." Mahendra ('36, p. 226) tells of his observation of the courtship
of *Hemidactylus flaviviridis*, and speaks of "...a low 'tak-tak-tak' sound," which he says they emit while chasing each other.

Bogert ('60, p. 145) states in his article on the influence of sound on Amphibians and Reptiles, that "...sound perception is subordinate in importance to vision or chemoreception in activities of most reptiles. Sound producing mechanisms are absent in the majority of species, but occur in some or all members of the four surviving Orders." In his introduction to this paper, he states that vocalizations such as the supposed mating call, are not made with forethought, design or intention. These vocalizations do not constitute speech as such, but can be thought of as being useful to the individual organism or to the species in its natural environment. He mentions that hearing in animals is underestimated and therefore neglected in many studies.
SUMMARY AND CONCLUSION

Morphologically, there appears to be no reason why the external and middle ear cannot function for the reception of air-vibrations in *Coleonyx variegatus*. However, even though the sound producing mechanism and the phonoreceptor have been described, further research will be needed before conclusions regarding the communicative value of these structures can be made. Visual, olfactory, and tactile stimulation, as well as hormonal influences, will have to be taken into account in demonstrating the value of sound to these animals.

Methods by which the tension of the tympanum is maintained as well as possible compensatory mechanisms by which the tympanum remains independent of the movement of the hyoid apparatus and tongue are proposed.

The significance of the break of the primary connection between hyoid and extracolumella is discussed, including a discussion of how the tympanum may have been formed in these animals, by separating off from the pharyngeal wall. Embryological studies may further strengthen this proposal. Parts of the insertion plate of the extracolumella which may be homologous to the processus internus and the
processus dorsalis of other lizards are discussed. Three possible mechanisms for the transmission of ground vibrations to the otic capsule are given.

Several morphological similarities between the geckos and pygopods are reviewed. It must be concluded, however, that similarities or differences with regard to the middle ear structure must be employed cautiously if at all in determining taxonomic affinities between these two groups. This is due primarily to the highly adaptive properties of the middle ear, and the fact that many similarities of this type may have arisen independently, perhaps through a process of parallel evolution. Mechanisms, using the middle ear of *Coleonyx variegatus* as perhaps being similar to that of a primitive gecko ancestral-type, are proposed for the adaptations of the middle ear which have taken place in burrowing-type lizards. The role that environmental stress may play in these types of adaptations are discussed.

The fact that the facial artery pierces the columella in both mammals and many geckos is mentioned, including a discussion of the possibility of its evolutionary significance.
LITERATURE CITED


28

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Figure 1. Ventral view of the pharyngeal cavity and upper palatal region with the floor of the pharynx and tongue removed. A--pharyngeal cavity; B--internal carotid artery; C--columella; D--pharyngeal wall.
Figure 2. Enlarged view of the extracolumellar insertion plate and columella. The facial artery pierces the footplate of the columella. A--fenestra rotunda; B--internal carotid artery; C--columella; D--facial artery; E--fenestra ovalis; F--pars inferiorus; G--pars accessorius anterior.
Figure 3. Lateral view of the pharyngeal wall and external ear. Skin and ventral hyoid musculature has been removed. A--capiti-cleido-episternalis; B--depressor mandibulae muscle; C--external auditory meatus; D--pharyngeal wall.
Figure 4. Diagram illustrating the tympanic compensation for tongue and hyoid movements. Depressor mandibulae and constrictor colli (superficial layer) muscles removed.